Environmental effects on photosynthetic capacity of bean genotypes

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Abstract – Photosynthetic responses to daily environmental changes were studied in bean (*Phaseolus vulgaris* L.) genotypes 'Carioca', 'Ouro Negro', and Guarumbé. Light response curves of CO_2 assimilation and stomatal conductance (g_s) were also evaluated under controlled (optimum) environmental condition. Under this condition, CO_2 assimilation of 'Carioca' was not saturated at 2,000 $\mu mol\ m^{-2}\ s^{-1}$, whereas Guarumbé and 'Ouro Negro' exhibited different levels of light saturation. All genotypes showed dynamic photoinhibition and reversible increase in the minimum chlorophyll fluorescence yield under natural condition, as well as lower photosynthetic capacity when compared with optimum environmental condition. Since differences in g_s were not observed between natural and controlled conditions for Guarumbé and 'Ouro Negro', the lower photosynthetic capacity of these genotypes under natural condition seems to be caused by high temperature effects on biochemical reactions, as suggested by increased alternative electron sinks. The highest g_s values of 'Carioca' were observed at controlled condition, providing evidences that reduction of photosynthetic capacity at natural condition was due to low g_s in addition to the high temperature effects on the photosynthetic apparatus. 'Carioca' exhibited the highest photosynthetic rates under optimum environmental condition, and was more affected by daily changes of air temperature and leaf-to-air vapor pressure difference.

Index terms: *Phaseolus vulgaris*, chlorophyll fluorescence, gas exchange, photosynthesis.

Efeitos ambientais na capacidade fotossintética de genótipos de feijoeiro

Resumo – Foram avaliadas as respostas fotossintéticas às variações diárias do ambiente nos genótipos de feijoeiro (*Phaseolus vulgaris* L.) 'Carioca', 'Ouro Negro' e Guarumbé. Curvas de resposta da assimilação de CO_2 e condutância estomática (g_s) à luz foram realizadas em condição ambiental controlada (ótima). Nessa condição a assimilação de CO_2 de 'Carioca' não foi saturada mesmo a 2.000 $\mu mol\ m^{-2}\ s^{-1}$, enquanto Guarumbé e 'Ouro Negro' apresentaram diferentes níveis de saturação lumínica. Os genótipos mostraram fotoinibição dinâmica e aumento reversível da fluorescência mínima da clorofila em condição natural, assim como menor capacidade fotosintética quando comparada à sob condição controlada. Uma vez que Guarumbé e 'Ouro Negro' apresentaram valores similares de g_s em ambas condições ambientais, a menor capacidade fotossintética desses genótipos sob condição natural parece ser causada pelos efeitos da alta temperatura nas reações bioquímicas, como sugerido pelo aumento dos drenos alternativos de elétrons. Os maiores valores de g_s em 'Carioca' foram observados em condição controlada, podendo a redução da capacidade fotossintética em condição natural ser atribuída aos baixos valores de g_s em adição aos efeitos da alta temperatura no aparato fotossintético. 'Carioca' exibiu as maiores taxas fotossintéticas em condições ambientais ótimas, sendo mais afetado pelas mudanças diárias de temperatura do ar e diferença de pressão de vapor folha-ar.

Termos para indexação: *Phaseolus vulgaris*, fluorescência de clorofila, fotossíntese, trocas gasosas.

Introduction

Among crops used in human alimentation, common bean has a great importance as a source of protein and energy (Dourado Neto & Fancelli, 2000). Due to the large cultivated area, bean plants are submitted to different environments with distinct air humidity, temperature, and irradiance levels (Singh, 1989), which affect the plant growth and productivity (Lopes et al., 1986). Photosynthesis is the main process responsible

for dry matter accumulation and consequently affects plant development and growth, being strongly regulated by the environment (McCree, 1986).

Stomatal conductance controls the photosynthesis (Farquhar & Sharkey, 1982; Jones, 1998), and stomatal behavior is influenced by both external and internal stimuli (Nobel, 1999). So, it could be expected negative stomatal effects on photosynthetic process in some conditions, when there is low air relative humidity or high air temperature. High temperature induces direct and indirect changes on bean photosynthesis, affecting directly the biochemical reactions (Pastenes & Horton, 1996a, 1996b) and causing stomatal closure (Comstock & Ehleringer, 1993) due to the increased air vapor pressure deficit. Both effects are always present in nature, where it is difficult to ascribe which one has more influence on leaf gas exchange.

The photochemical activity is also affected by environmental stresses (Van Kooten & Snel, 1990; Maxwell & Johnson, 2000), such as high temperature (Yamane et al., 1997; Costa et al., 2002). Photochemical reactions are linked to the CO_2 fixation process by supplying ATP and NADPH, and are also regulated by alternative electron sinks, such as photorespiration, Mehler reaction and nitrogen reduction (Champigny, 1995; Cornic & Fresneau, 2002; Noctor et al., 2002). In addition to the effect of high temperature (Pastenes & Horton, 1996b; Yamane et al., 1997; Pastenes & Horton, 1999), the photochemical apparatus may also be influenced by high light intensity (Long et al., 1994; Osmond, 1994; Critchley, 1998), which frequently occurs around noon when air temperature and vapor pressure deficit are elevated. Concerning the effects of elevated air temperature in bean plants, Pastenes & Horton (1996b) and Costa et al. (2002) observed that the susceptibility of photosynthetic apparatus depends on studied genotype. Therefore, bean cultivars show different physiological responses when submitted to the same changes in air temperature and vapor pressure deficit. In fact, these responses permit genotypes to avoid or tolerate high temperature effects, allowing plants to maintain adequate or reasonable photosynthetic rates (Pastenes & Horton, 1996a, 1996b, 1999; Costa et al., 2002).

Daily environmental changes of air temperature, vapor pressure deficit, and irradiance may occur simultaneously, affecting plant species in different degrees. Thus, the overall effect is not a sum of isolate influences of each environmental constraint, but rather a synergetic effect. Regardless the water deficit effects on bean physiology (Pimentel et al., 1999a, 1999b; Souza et al., 2003), studies involving the impacts of natural environmental fluctuation on the physiology of different bean genotypes have not been reported. Greater knowledge on how plants respond to natural environmental changes and how they are affected may improve crop management and show some guidelines for bean breeding programs in regions with specific environmental characteristics.

The objective of this work was to evaluate the effects of daily environmental changes on photosynthetic capacity of bean (*Phaseolus vulgaris* L.) genotypes 'Carioca', 'Ouro Negro' and the landrace Guarumbé.

Material and Methods

Five bean seeds (*Phaseolus vulgaris* L.) of genotypes 'Carioca', 'Ouro Negro', and Guarumbé were sown in 10 L pots, containing the substrate Plantmax. After seed germination, two plants were kept per pot. Seedlings were grown under greenhouse condition, where there was maximal irradiance intensity at about 1,800 $\mu mol\ m^{-2}\ s^{-1}$, air temperature from 44ºC to 18ºC, and RH between 30 and 100%. A nutrient solution (McCree, 1986) was applied at sowing and 15 days after seedling emergence (DAE) to ensure that no nutritional deficiency would occur. Plants were watered daily (except during fertirrigation).

Measurements of leaf gas exchange were taken in completely expanded and exposed leaves at 25 DAE, using the LICOR LI-6400 infrared gas analyzer. The CO_2 and water vapor fluxes were measured and the CO_2 assimilation (A) and transpiration (E) rates, stomatal conductance (g_s), and intercellular CO_2 concentration (Ci) were calculated by the LI-6400 data analysis program according to Von Caemmerer & Farquhar (1981).

Chlorophyll a fluorescence was measured with the Hansatech FMS1 modulated fluorometer, wherein the maximal (F_m) and minimum (F_o) fluorescence yields were obtained in dark-adapted (30 min) leaves, and steady-state (F_s) and maximal (F_m') fluorescence yields were measured in light-adapted leaves (Van Kooten & Snel, 1990). Thus, variable fluorescence yield was determined in dark-adapted ($F_v = F_m - F_o$) and in light-adapted ($\Delta F = F_m' - F_s$) states. F_o' is the minimum

fluorescence yield after photosystem I excitation by far-red light. The following parameters were calculated: the potential (F_v/F_m) and effective ($\Delta F/F_m'$) quantum efficiency of photosystem II (PSII), and the apparent electron transport rate [ETR = ($PPFD \times \Delta F/F_m' \times 0.5 \times 0.84$)] (Schreiber et al., 1994). For the calculation of ETR, the fraction of excitation energy distributed to PSII used was 0.5, and the fractional photosynthetic photon flux density (PPFD) absorption used was 0.84 (Demmig & Björkman, 1987). The alternative electron sinks (AES) were estimated as the relation between $\Delta F/F_m'$ and the quantum efficiency of CO_2 assimilation [$\Phi CO_2 = A/(PPFD \times 0.84)$] (adapted from Edwards & Baker, 1993).

Seven days after transferring plants from greenhouse to full sunlight condition (open area in Piracicaba, SP, Brazil, 22º42'S, 47º30'W, 576 m of altitude) characteristic of summer season, the measurements of leaf gas exchange and chlorophyll a fluorescence were taken in the same leaf, in intervals of approximately 1.5 hours between 6 am and 6 pm. The leaf water potential (Ψ_w) was measured by the psychometric method, operating in hygrometric dew point mode, with the Wescor HR-33T microvoltmeter and Wescor C-52 sample chambers at pre-dawn and at 1:30 pm. Environmental variables were monitored by the LI-6400, with PPFD, air temperature (T_{air}) and leaf-to-air vapor pressure difference ($VPD_{leaf-air}$) recorded at same time of the physiological measurements.

Photosynthetic capacity (PC) under optimum environmental condition was determined through light response curves of A and g_s at controlled condition, with leaf temperature of 25ºC and air vapor pressure deficit (VPD) around 1.0 kPa. Leaf temperature was controlled by the LI-6400 and VPD by the LICOR LI-610 dew point generator attached to the LI-6400. Both values of leaf temperature and VPD are considered to be optimum to the photosynthetic activity and to prevent stomatal closure respectively (Jones, 1971; Comstock & Ehleringer, 1993). Light response curves of A and g_s were obtained varying PPFD from 2,000 to 0 $\mu mol\ m^{-2}\ s^{-1}$.

The experiment was arranged in a completely randomized block design, with three and six replications, at controlled and natural conditions, respectively, sampled in different plants. Data were subjected to analysis of variance (ANOVA) and the mean values were compared by Tukey's test at the 0.05 probability level.

Results and Discussion

The highest values of T_{air}, $VPD_{leaf-air}$ and PPFD were observed in the afternoon (1:17 pm), with values of T_{air} higher than 38ºC, $VPD_{leaf-air}$ of 3.7 kPa and PPFD around 2,000 $\mu mol\ m^{-2}\ s^{-1}$ (Figure 1).

Daily course of CO_2 assimilation (A) was similar for all evaluated genotypes (Figure 2). In early morning, the sharp increase in photosynthetic photon flux density (PPFD) seems to be the main cause of A increases. Considering the highest A values, no statistical difference was found between bean genotypes under natural condition. Maximal A rates were reached around 8:45 am and maintained until 11:45 am when reductions in stomatal conductance (g_s) were caused by increasing leaf-to-air vapor pressure difference ($VPD_{leaf-air}$) (Figure 2). Low g_s is known to cause decrease in A by reducing the CO_2 available, which may be indicated by decreased intercellular CO_2 concentration (Ci) values (Jones, 1998; Nobel, 1999). Nevertheless, relatively stable Ci values from 8:35 am to 3:09 pm suggested that stomatal closure was not the main cause of reductions in A in that time (Figure 2). Hence, it could be inferred that the high air temperature (higher than 36ºC) caused increase in photorespiration and consequent reduction in the photosynthetic activity, as indicated by increased alternative electron sinks (AES) (Figure 3).

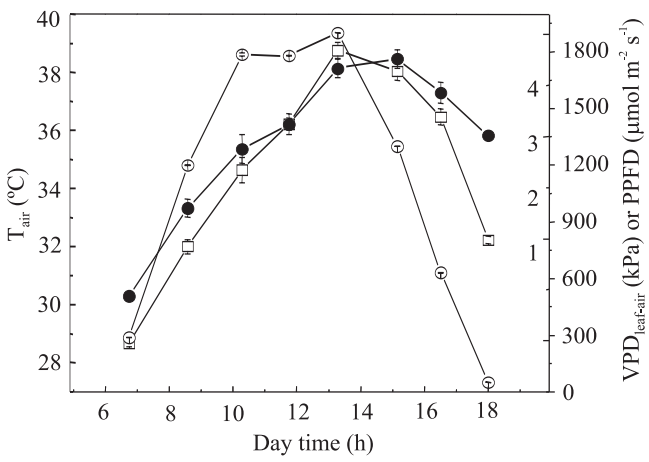

Figure 1. Daily courses of air temperature (T_{air}: □), leaf-to-air vapor pressure difference ($VPD_{leaf-air}$: ●) and photosynthetic photon flux density (PPFD: ○) at full sunlight condition in summer season of Piracicaba, SP, Brazil. Each point represents the mean±standard error of 18 replications.

Stomata showed a slight opening tendency until 11:45 am, when decreases in g_s were likely due to high transpiration (E) values (Figure 2). Increases in E were caused by an elevation of $VPD_{leaf\text{-}air}$, which induced reductions in Ψ_w (Table 1). Since similar g_s values were observed during morning, changes in E values suggest that stomatal aperture was more than sufficient to support maximal E values since early hours of morning.

The photochemical apparatus of bean genotypes was also affected by environmental conditions (Figure 4). High PPFD levels caused photoinhibition in all genotypes. Photoinhibition is recognized by decreases in the quantum efficiency of PSII and indicated by F_v/F_m values below to 0.725 (Critchley, 1998), being caused by excessive light energy (Long et al., 1994).

The lowest F_v/F_m values were observed at 11:45 am in all genotypes, but different photoinhibition recovery capacities were observed among 'Carioca', Guarumbé and 'Ouro Negro' (Figure 4). Guarumbé was most affected by excessive light energy, being the last genotype to initiate the photoinhibition recovery (at 4:30 pm), whereas 'Ouro Negro' and 'Carioca' exhibited F_v/F_m recovery from 11:45 am and 1:17 pm, respectively.

The photoinhibition mechanism could have a character of photoprotection or represent damaging in PSII reaction centers (Osmond, 1994). The former is associated to an avoidance of over-excitation of the PSII reaction center by decreased energy absorption or by increased thermal dissipation of excitation energy via xanthophyll cycle, and the later is related to a cycle of PSII reaction center inactivation and repair (Demmig-Adams III & Adams III, 1992; Long et al., 1994; Osmond, 1994; Critchley, 1998). In this study, all genotypes exhibited dynamic photoinhibition, i.e., a photoprotective mechanism (Osmond, 1994).

Increases in PPFD also caused reductions in $\Delta F/F_m'$, when the lowest values were observed after midday in all genotypes (Figure 4). As expected, an inverse pattern was observed between apparent electron transport rate

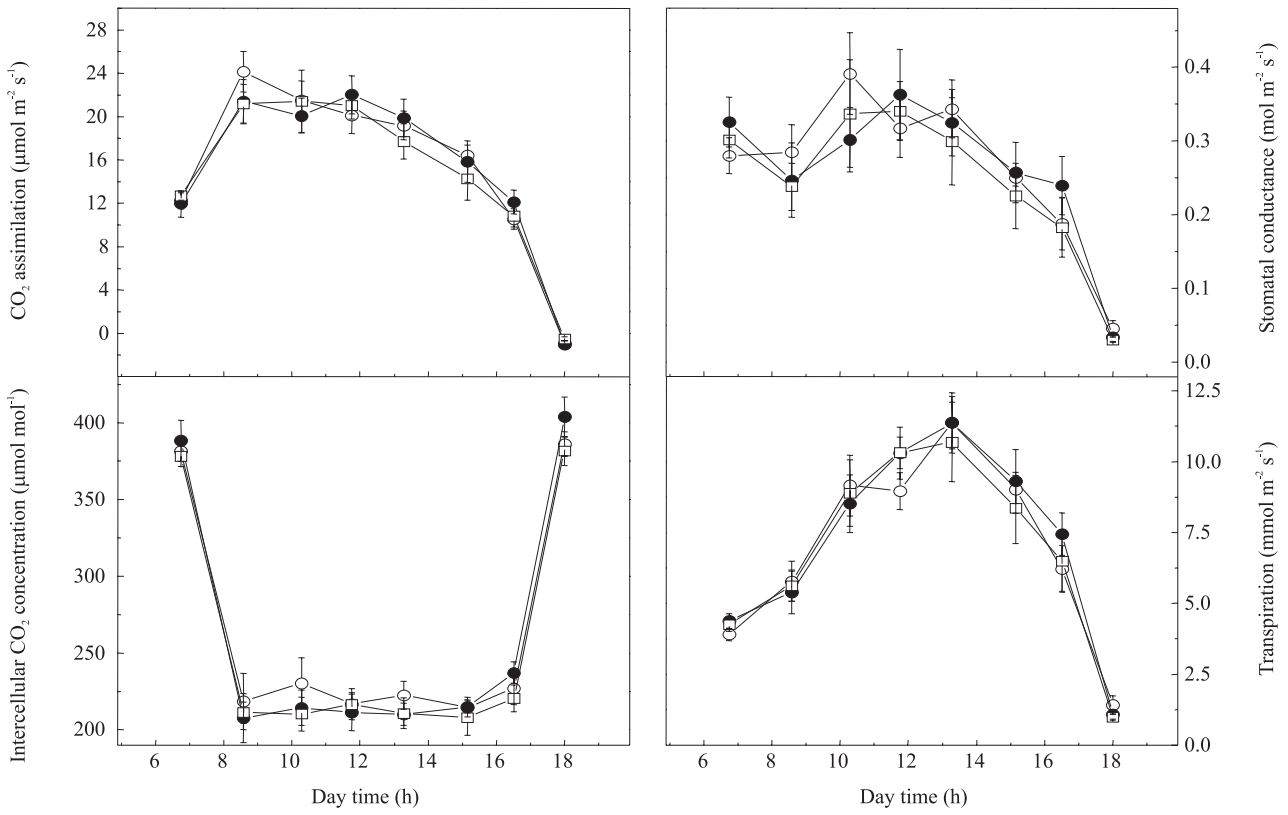

Figure 2. Daily courses of CO_2 assimilation, stomatal conductance, intercellular CO_2 concentration, and transpiration in bean genotypes 'Carioca' (○), Guarumbé (●), and 'Ouro Negro' (□) exposed to daily changes of environmental variables in Piracicaba, SP, Brazil. Each point represents the mean±standarderror of six replications.

(ETR) and effective quantum efficiency of PSII ($\Delta F/F_m'$), with the highest ETR values coinciding with the highest A values (Figures 2 and 4). According to Maxwell & Johnson (2000), $\Delta F/F_m'$ is related to the proportion of light absorbed by chlorophyll molecules and used in photochemistry, and its decrease is associated to reaction center closure and thermal energy dissipation processes.

Besides the effects of high irradiance on photosynthesis, plants were also subjected to high air temperature, and this factor is known to cause impairments on photosynthetic apparatus (Berry & Björkman, 1980). Decrease in F_v/F_m with simultaneous increase in F_o is an indicator of damage in PSII caused by high temperatures (Pastenes & Horton, 1996a, 1999; Yamane et al., 1997). This pattern was observed in all genotypes, which exhibited the highest F_o values at 11:45 am (Figure 5), when air temperature was close to 36ºC (Figure 1). The F_o is related to the size of chlorophyll antenna and the rate of thermal deactivation of inhibited PSII centers (Krause & Weis, 1991). According to Yamane et al. (1997), increase in the F_o level is caused partly by reversible inactivation of the PSII reaction center at high temperatures. Moreover, Öquist et al. (1992) have associated increases in F_o with protective or regulatory processes that take place at PSII.

Although photochemical reactions had been affected by daily environmental changes (Figures 4 and 5), CO_2 assimilation was not affected by reductions in photochemical activity and genotypes showed similar maximum rates between 8:35 am and 11:45 am (Figure 2). Under controlled condition, bean genotypes exhibited distinct photosynthetic capacities, i.e., maximum photosynthetic rates (Figure 6), which were not observed under natural condition (Figure 2). Photosynthetic capacity (PC) was higher in 'Carioca' (35 μmol m^{-2} s^{-1}) than in the other genotypes, exhibiting non-saturation even at 2,000 μmol m^{-2} s^{-1} (Figure 6). 'Ouro Negro' showed PC around 25 μmol m^{-2} s^{-1} and light saturation at 2,000 μmol m^{-2} s^{-1}, whereas Guarumbé was not fully saturated and presented PC around 30 μmol m^{-2} s^{-1}. The maximum CO_2 assimilation values observed are in agreement with the measurements performed by Von Caemmerer & Farquhar (1981), Comstock & Ehleringer (1993) and Souza et al. (2003) in common bean genotypes. Different photosynthetic capacities between bean cultivars may be caused by differences in carboxylation capacity and protein content (Evans, 1989), as well as by different number of mesophyll cells per unit surface leaf area (Nobel, 1999).

Considering maximal A rates in both experimental conditions, 'Carioca' genotype was more affected by daily changes of environmental variables, showing a reduction of 43%. Guarumbé and 'Ouro Negro' exhibited decreases around 33% and 20%, respectively (Figure 6). Stomatal closure could be a cause of PC reduction in 'Carioca' since lower g_s values were observed under natural condition. The high g_s similarity in 'Ouro Negro' and Guarumbé, when considered both experimental conditions, indicated non-stomatal restriction of PC under natural condition.

Besides g_s effects (Farquhar & Sharkey, 1982; Jones, 1998; Nobel, 1999), high temperatures also cause impairments in photochemical and biochemical reactions

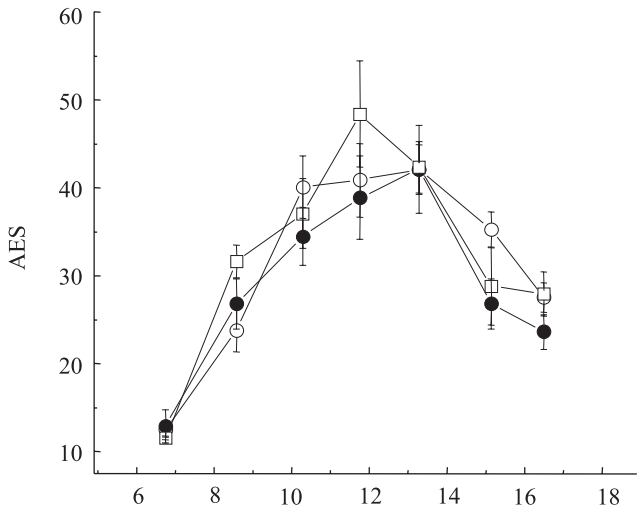

Figure 3. Daily course of alternative electron sink (AES) in bean genotypes 'Carioca' (○), Guarumbé (●) and 'Ouro Negro' (□) exposed to daily changes of environmental variables in Piracicaba, SP, Brazil. Each point represents the mean±standarderror of six replications.

Table 1. Leaf water potential (MPa) of bean genotypes 'Carioca', Guarumbé, and 'Ouro Negro' measured at pre-dawn and at 1:30 pm in plants exposed to full sunlight condition, in Piracicaba, SP, Brazil[(1)].

Day time	Bean genotype		
	'Carioca'	Guarumbé	'Ouro Negro'
Pre-dawn	-0.24±0.10aA	-0.24±0.03aA	-0.23±0.04aA
1:30 pm	-1.37±0.14aB	-1.37±0.28aB	-1.40±0.04aB

[(1)]Data represent the mean±standart error of 4 replications; different small letters in line and capital letters in column show significant difference by Tukey's test at the 0.05 probability.

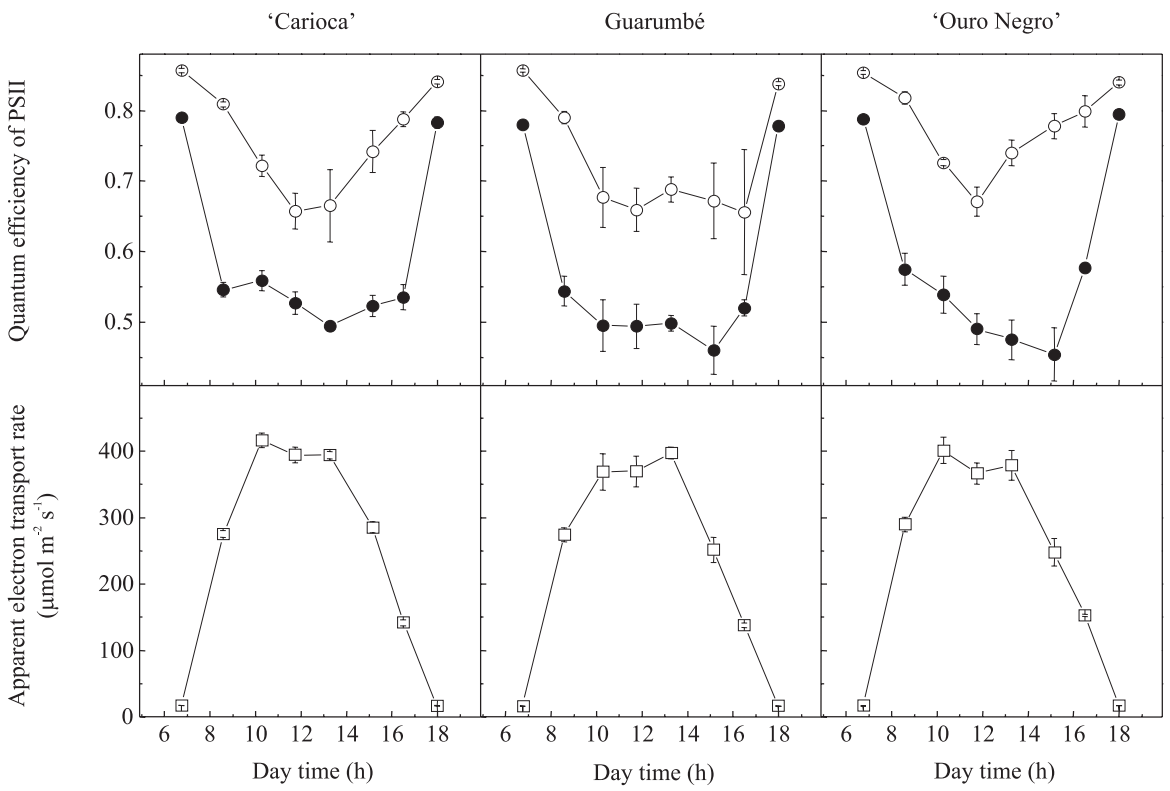

Figure 4. Daily courses of potential (○) and effective (●) quantum efficiency of photosystem II (PSII) and apparent electron transport rate (□) in bean genotypes 'Carioca', Guarumbé, and 'Ouro Negro' exposed to daily changes of environmental variables in Piracicaba, SP, Brazil. Each point represents the mean±standard error of three (○) and six (● and □) replications.

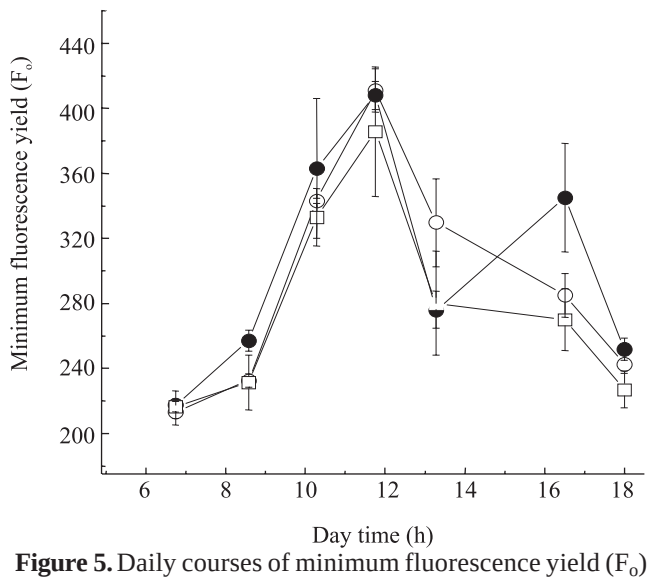

Figure 5. Daily courses of minimum fluorescence yield (F_o) in bean genotypes 'Carioca' (○), Guarumbé (●) and 'Ouro Negro' (□) exposed to daily changes of environmental variables in Piracicaba, SP, Brazil. Each point represents the mean±standard error of six replications.

of photosynthesis (Berry & Björkman, 1980; Pastenes & Horton, 1996a, 1996b, 1999; Costa et al., 2002). Therefore, the results suggest that the PC of 'Carioca' was constrained at natural condition by low g_s and high temperature, whereas 'Ouro Negro' and Guarumbé had their PC impaired only by high temperature.

All genotypes showed a reversible increase in AES, which was probably caused by increased leaf temperature during daylight period. Among alternative electron sinks, photorespiration is the most important (Cornic & Fresneau, 2002), acting as a sink for reducing equivalents (e.g. NADPH) and ATP, as well as playing an important role on protection of photosynthetic apparatus from the deleterious effects of excessive light energy (Osmond & Björkman, 1972). Thus, plant photosynthesis can be decreased by increases in photorespiration under high temperature (Monson et al., 1982; Kobza & Edwards, 1987). Higher photorespiratory rates could be explained by increase in the O_2/CO_2 solubility ratio and in oxygenase activity of Rubisco induced by high

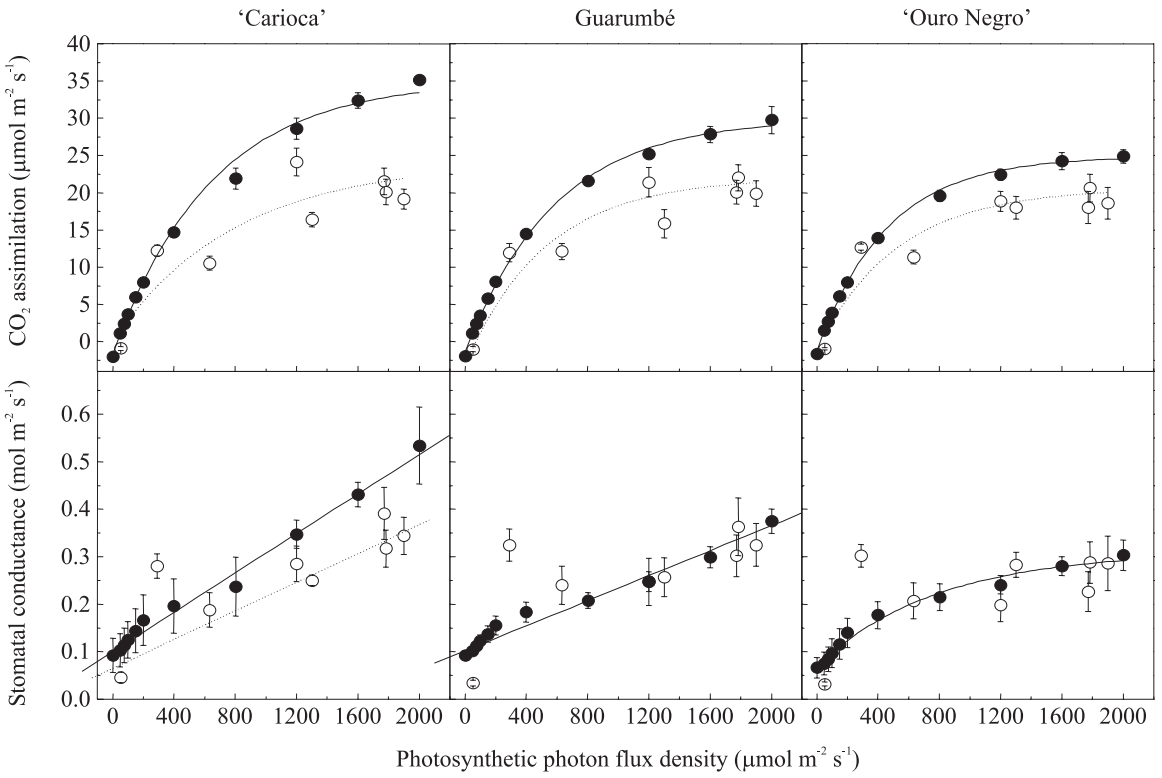

Figure 6. Light response curves of CO_2 assimilation and stomatal conductance of bean genotypes 'Carioca', Guarumbé, and 'Ouro Negro' exposed to daily changes of environmental variables in Piracicaba, SP, Brazil (○) and exposed to optimum environmental condition (●). Each point represents the mean ± standard error value of six (○) and three (●) replications.

temperatures (Ku & Edwards, 1977; Bernacchi et al., 2001). Therefore, it would be expected negative effects on photosynthesis since T_{leaf} was higher than 36ºC in the afternoon and the optimum temperature for bean growth and photosynthesis is around 25ºC (Jones, 1971; Singh, 1989).

Results indicated that the photosynthetic capacity of 'Carioca' was reduced by low g_s values and increased AES under natural condition, whereas 'Ouro Negro' and Guarumbé were affected only by increased AES (Figures 3 and 6). Higher susceptibility of the genotype 'Carioca' to high $VPD_{leaf-air}$ and temperature (low g_s and high AES, respectively) is in agreement with previous reports that indicated 'Carioca' as an improper genotype for regions with high T_{air} and VPD (Masaya & White, 1991; Costa et al., 2002). However, this genotype may be very useful in breeding programs for increase photosynthetic capacity, since the highest CO_2 assimilation values were observed in 'Carioca' under optimum environmental condition.

Conclusion

1. When compared with 'Ouro Negro' and Guarumbé, 'Carioca' exhibits the highest photosynthetic capacity under optimum environmental condition.

2. 'Carioca' photosynthetic rate is more affected by daily changes of air temperature and leaf-to-air vapor pressure difference.

Acknowledgements

To Fapesp (Fundação de Amparo à Pesquisa do Estado de São Paulo, Brazil), Capes (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil), and to CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil), for fellowships granted.

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Received on October 20, 2003 and accepted on April 26, 2004